SURVIVORSHIP AND GROWTH OF GIANT SEQUOIA (*SEQUOIADENDRON GIGANTEUM* (LINDL.) BUCHH.) SEEDLINGS AFTER FIRE

H. THOMAS HARVEY[1]
H. T. Harvey and Associates,
P.O. Box 1180, Alviso, CA 95002

HOWARD S. SHELLHAMMER
Department of Biological Sciences, San Jose State University,
San Jose, CA 95192

ABSTRACT

Fire has long been thought to play an important role in the reproduction of the giant sequoia (*Sequoiadendron giganteum*). In this 20 year study the efficacy of fire in promoting reproduction and growth are quantified. Findings are reported on growth and survival of seedlings that first developed in 1966 through 1968 after experimental burns in Kings Canyon National Park. Seedlings growing on substrates beneath former burn piles were significantly taller in their later years than those on scarified substrates. Seedlings that grew on substrates that had been beneath piles of burned logs had significantly higher survival rates than did those on all other substrates during the early years of seedling life.

The giant sequoia (*Sequoiadendron giganteum*) is the largest living thing known to ever exist on Earth. Formerly widely distributed, it is now restricted in its native range to the west slope of the Sierra Nevada of California. Its reproduction has long been associated with fire (Muir 1878), which is needed to remove surface litter and duff and open up the canopy (Kilgore and Biswell 1971). When hot fires burn in dense stands of mature giant sequoias as many as 100,000 seedlings per hectare may develop following heat-induced seed fall (Hartesveldt et al. 1975). It has been noted that few to no seedlings become established in unburned areas (Kilgore and Biswell 1971; Hartesveldt and Harvey 1967; Hartesveldt et al. 1975; Harvey et al. 1980). This study reports giant sequoia seedling growth and survivorship relative to fire intensity after the first experimental fires in a coniferous forest ecosystem in a western National Park.

METHODS

Four study areas were established in the Redwood Mountain Grove of giant sequoias in Kings Canyon National Park in 1964, 1965, and 1966. Logs and felled snags were cut into sections, piled, and

[1] Tom Harvey died August 1, 1990; address correspondence to H. Shellhammer.

MADROÑO, Vol. 38, No. 1, pp. 14–20, 1991

burned in Trail Area in 1965 and in South Area in 1966. The heavy equipment used to move the logs often exposed mineral soil (scarified substrate). In other areas mineral soil was not exposed and had enough fuel to carry a surface fire (burned substrate). A few patches were a mix of scarified and heated substrates. In the first few years following these treatments thousands of giant sequoia seedlings germinated on the forest floor. Six substrates were recognized: 1) rotten logs, 2) burned surface, 3) scarified surface, 4) mixed burned and scarified surfaces, 5) fire breaks (hand cleared strips of mineral soil around the burn/manipulated portion of each study area), and 6) surface burned beneath log piles; substrates 1 and 5 are not reported on in this paper. Temperatures beneath burned log piles reached 600 degrees F from 2.5 to 7.5 cm below the soil surface (Hartesveldt and Harvey 1967).

Over 7000 seedlings were individually identified by number and then counted at each of the sites during various years (Tables 1 and 2). The survival rates of sequoia seedlings were calculated as seedling density (#/ha). The number of seedlings surviving in years when counts were not taken were interpolated from survival curves. Because the initial density of seedlings varied between substrate conditions, seedling density was standardized with a starting density of 1000 seedlings/ha.

We used a linear regression analysis to determine whether density dependent differences in survival as a result of different starting seedling density was influencing the survival between substrate conditions. The frequency distributions of the number of seedlings surviving between substrates for each cohort each year were analyzed with a G-test (Pyke and Thompson 1986). Simultaneous pairwise test procedures between substrate conditions at the Trail site followed Sokal and Rohlf (1981). Growth rate was measured as increase in seedling height.

Results

There was no significant relationship between the starting density of sequoia seedlings and the average annual survival rate ($F = 0.008$, $df = 11$, $p = 0.987$) or the proportion surviving in 1986 ($F = 0.0631$, $df = 1$, $p = 0.977$). This indicated that the differences we observed in the survival of sequoia seedlings were due to differences in substrate and not to density dependent effects.

The survival of sequoia seedlings on burn piles for the Trail 1966 cohort was significantly greater than that on the other substrates each year ($p < 0.001$) (Table 1). The overall annual average survival of seedlings on burn piles was 2.5–3.5× greater than on the other substrates ($G = 2470.3$, $df = 3$, $p < 0.0000$). The survival of seedlings on surface burn/scarified substrate was significantly greater than

TABLE 1. SURVIVABILITY OF GIANT SEQUOIA SEEDLINGS ON FOUR SUBSTRATES AT TRAIL AREA, KINGS CANYON NATIONAL PARK, 1966–1986. Seedling survival rates were calculated from seedling densities counted in 1966, 1967, 1969, 1974, 1979, and 1986 and are noted here by *. Survival rates for the intervening years were interpolated from the observed survival curve, and since the starting seedling densities varied between substrate conditions the survival rates were adjusted to a starting density of 1,000 seedlings. * = years when seedlings were counted. ** Surf. burn = surface burn, S.B./Scar. = mixture of surface burn and scarified surface, Scar. = scarified surface.

	1966 Cohort				1967 Cohort			
Year	Burn** pile	Surf. burn	S.B./ Scar.	Scar.	Burn pile	Surf. burn	S.B./ Scar.	Scar.
1966*	1000	1000	1000	1000				
1967*	273	20	69	36	1000	1000	1000	1000
1968*	273	20	64	36	190	74	65	110
1969*	273	18	61	36	171	15	22	29
1970	252	16	55	31	160	14	17	26
1971	232	15	51	27	149	13	17	22
1972	212	13	48	20	138	11	13	18
1973	212	11	43	18	126	11	9	17
1974*	212	11	41	16	115	11	4	16
1975	188	8	36	14	112	10	0	15
1976	164	6	35	13	108	9	0	14
1977	139	5	31	12	104	8	0	13
1978	115	3	30	11	100	7	0	12
1979*	91	0	25	9	97	6	0	11
1980	87	0	23	9	93	5	0	11
1981	82	0	23	8	89	5	0	10
1982	78	0	22	8	86	5	0	10
1983	74	0	20	8	82	5	0	9
1984	70	0	18	7	78	4	0	9
1985	65	0	16	7	74	3	0	9
1986*	61	0	16	7	71	3	0	8

seedlings on surface burn substrate during all years ($p < 0.0001$), and significantly greater than seedlings on scarified substrate from 1967–1986. The survival of seedlings on scarified substrate was greater than on surface burn substrate from 1967–1970 ($p < 0.0290$) and from 1978–1986 ($p < 0.0203$).

The survival of sequoia seedlings on burn piles for the Trail 1967 cohort was significantly greater than that on the other substrates each year ($p < 0.0001$) (Table 1). The overall annual average survival of seedlings on burn piles was 2.5× greater than on the other substrates ($G = 2470.3$, $df = 3$, $p < 0.0001$). The survival of seedlings on surface burn substrate was significantly greater than seedlings on surface burn/scarified substrate from 1975–1986 ($p < 0.0393$). The survival of seedlings on scarified substrate was significantly greater

TABLE 2. SURVIVABILITY OF GIANT SEQUOIA SEEDLINGS ON TWO SUBSTRATES AT SOUTH AREA, KINGS CANYON NATIONAL PARK, 1967–1986. Seedling survival rates were calculated from seedling densities counted in 1968, 1969, 1974, 1979, and 1986 and are noted here by *. Survival rates for the intervening years were interpolated from the observed survival curve, and since the starting seedling densities varied between substrate conditions the survival rates were adjusted to a starting density of 1,000 seedlings. * = years when seedlings were counted.

	1967 Cohort		1968 Cohort	
Year	Burn pile	Scarified	Burn pile	Scarified
1967*	1000	1000		
1968*	699	337	1000	1000
1969*	497	117	733	465
1970	477	79	673	333
1971	431	67	614	266
1972	386	39	554	199
1973	366	26	495	134
1974*	314	22	435	125
1975	310	20	424	119
1976	306	18	412	114
1977	301	18	401	104
1978	297	16	390	97
1979*	294	14	379	93
1980	288	14	361	92
1981	284	14	344	87
1982	279	12	325	82
1983	275	10	308	77
1984	271	10	290	72
1985	266	8	272	67
1986*	261	8	255	62

than on surface burn from 1968–1969 ($p < 0.0316$) and significantly greater than surface burn/scarified in all years except 1969–1973 ($p < 0.0001$).

For both the South 1967 and South 1968 cohorts, the survival of sequoia seedlings on burn piles was significantly greater than on scarified substrate in all years ($p < 0.0001$) (Table 2). The average annual survival of sequoia seedlings on burn piles for the South 1967 cohort was 4× greater than seedlings on scarified substrate ($G = 3758.6$, $df = 1$, $p < 0.0001$), while it was 2.5× greater for seedlings on burn piles for the South 1968 cohort ($G = 1982.2$, $df = 1$, $p < 0.0001$).

The height growth of sequoia seedlings was significantly greater on burn pile substrates than on other substrates in South Area but not in Trail Area (Figs. 1 and 2). Heights of the 1967 cohort in South Area were not measured until 1972 but by then seedlings on burn piles were significantly taller than seedlings on scarified substrates. The difference increased as time passed (Fig. 1). The 1968 cohort

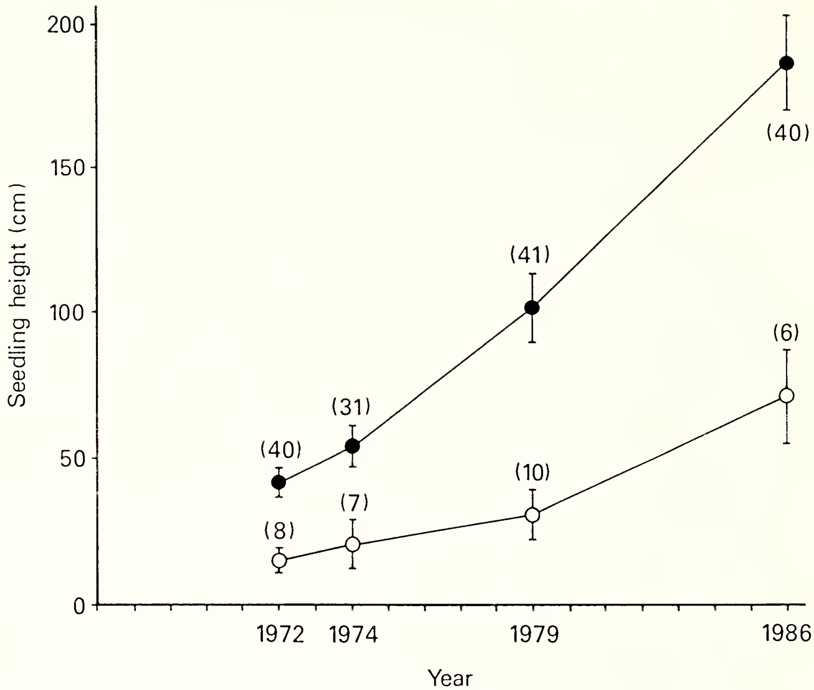

FIG. 1. Comparative growth of the South Area 1967 cohort of giant sequoia seedlings burn pile surfaces (●) versus seedlings on scarified substrate (○). Each point represents the mean height for (n) individuals ± one standard error. The results of the treatments were statistically different ($p < 0.05$) for each age class.

of South Area showed a similar pattern with a significant difference evident within four years of germination. The difference steadily increased through the years (Fig. 2).

DISCUSSION

Results of studies of four cohorts of giant sequoia seedlings indicate that seedlings which become established on burn pile soils survive better than those on other substrates during the first few years. Our results also suggest that the hottest fires, in this case produced by logs which were piled and burned, bring about soil conditions that are most favorable to the survival and growth of giant sequoia seedlings. Most of the burn piles were placed away from the canopy of nearby giant sequoias to reduce potential damage to the trees, hence seedlings growing on burn piles received considerable sunlight. Stark (1968) noted that giant sequoia seedlings grew best in full sunlight. In general, heated soils are known to increase in wettability; heated soils are also more friable after heating than

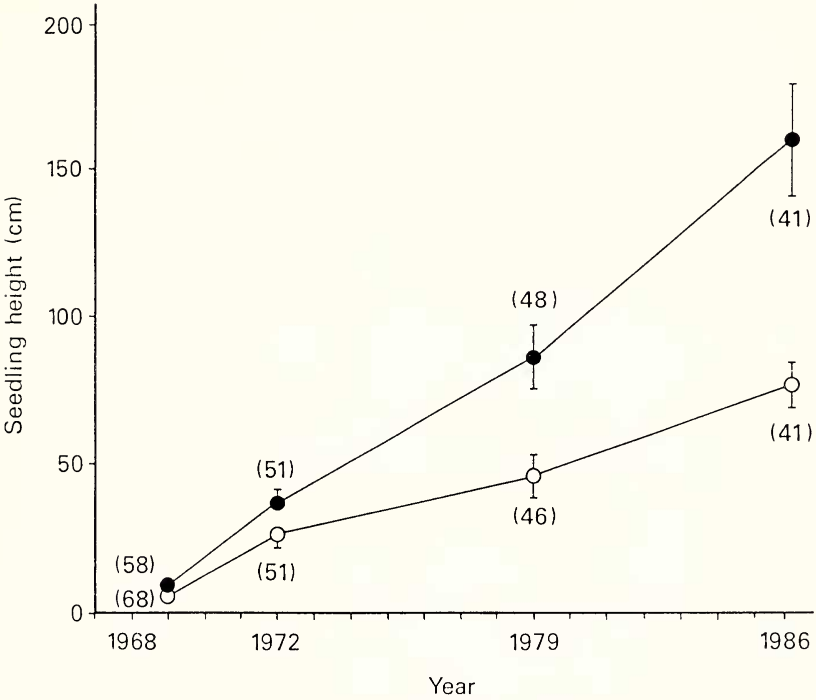

FIG. 2. Comparative growth of the South Area 1968 cohort of giant sequoia seedlings on burn pile substrates (●) versus seedlings on scarified substrates (○). Each point represents the mean height of (n) individuals ± one standard error. The results of the treatments were statistically different ($p < 0.05$) for each age class, except 1969.

before (Donaghey 1969). The killing of seeds of competing species and pathogens in the soil by heat favors the survival of giant sequoia seedlings. The giant sequoia seeds fall on the soil in large numbers after the heat of the fire has caused the serotinous cones to open (Hartesveldt et al. 1975). Thus the fire that clears the forest floor of litter and duff and kills competing species' seeds and pathogens, also kills the cone-bearing branches thus inducing a virtual rain of giant sequoia seeds from once closed cones (Harvey et al. 1980). The seeds fall upon an ideal seedbed and if the soil moisture is correct a carpet of seedlings is born.

ACKNOWLEDGMENTS

We thank Ron and Phyllis Stecker for help in the field. Bruce Kilgore, Wanna Pitts, and Dick Mewaldt critically reviewed early drafts for which we are grateful. Mike Kutilek and Rob Klinger provided invaluable statistical help; without Rob's help after the death of Tom Harvey, this paper could not have been completed.

Literature Cited

DONAGHEY, J. L. 1969. The properties of heat soils and their relationships to giant sequoia germination and seedling growth. M.A. Thesis. San Jose State Univ., San Jose, CA. 173 pp.

HARTESVELDT, R. J. and H. T. HARVEY. 1967. The fire ecology of Sequoia regeneration. Tall Timbers Fire Ecol. Conf. 7:65–77.

———, ———, H. S. SHELLHAMMER, and R. E. STECKER. 1975. The Giant Sequoia of the Sierra Nevada. U.S.D.I., Nat. Park Serv., Washington, DC. 180 pp.

HARVEY, H. T., H. S. SHELLHAMMER, and R. E. STECKER. 1980. Giant Sequoia Ecology. U.S.D.I., Nat. Park Serv., Washington, DC. 182 pp.

KILGORE, B. M. and H. H. BISWELL. 1971. Seedling germination following fire in a giant sequoia forest. Calif. Agric. 25:8–10.

MUIR, J. 1878. The new sequoia forests of California. Harpers 57:813–827.

PYKE, D. A. and J. N. THOMPSON. 1986. Statistical analysis of survival and removal rate experiments. Ecology 67:240–245.

SOKAL, R. R. and F. J. ROHLF. 1981. Biometry. W. H. Freeman, San Francisco. 859 pp.

STARK, N. 1968. The environmental tolerance of the seedling stage of *Sequoiadendron giganteum.* Amer. Midl. Nat. 80:84–95.

(Received 24 Apr 1990; revision accepted 12 Oct 1990.)